

USE, MANAGEMENT AND DOMESTICATION OF COLUMNAR CACTI IN SOUTH-CENTRAL MEXICO: A HISTORICAL PERSPECTIVE

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ABSTRACT.— Ethnohistorical and ethnobotanical information on columnar cactus species utilized and managed by peoples of the south Pacific slope in south-central Mexico is presented. This region comprises the highest diversity of species of columnar cacti in the world, with 45 of the 70 Mexican species of Pachycereeae and Cereeae, all of them being useful species. Although columnar cacti have been used by local people for thousands of years, no archaeological or historical records have been found on human manipulation of these plants in the past. At present, most of the columnar cactus species are only gathered from wild populations, but wild populations of 18 species are managed *in situ* and 12 species are cultivated. Quality and availability of useful products, their importance in human subsistence and the viability of manipulation of plants are all factors influencing the way of management of columnar cacti. The pattern of domestication *ex situ* and *in situ* acting simultaneously, observed in *Stenocereus stellatus* is hypothesized to occur also in other columnar cactus species with relatively fast growth and vegetative propagation, whereas a pattern of domestication *in situ* acting alone is hypothesized to occur in giant columnar cactus species. Comparative biological studies of wild and manipulated populations could give information on trends and extent of changes under domestication and, then, to lead to a better understanding on the nature and antiquity of the process.

Key words: columnar cacti, domestication, ethnobotany, Mixteca, Tehuacán Valley

RESUMEN.— Se presenta información etnohistórica y etnobotánica sobre las especies de cactáceas columnares utilizadas y manejadas por pueblos indígenas de la vertiente del Pacífico Sur de México. Esta región comprende la mayor diversidad de especies de cactáceas columnares del mundo, con 45 de las 70 especies mexicanas de Pachycereeae y Cereeae, la totalidad de las cuales son especies útiles. Aunque las cactáceas columnares han sido usadas por la gente de la región durante miles de años, no se han encontrado registros arqueológicos o históricos sobre su manipulación por seres humanos en el pasado. En la actualidad, la mayor parte de las especies de cactáceas columnares son exclusivamente

recolectadas a partir de poblaciones silvestres. No obstante, poblaciones silvestres de 18 especies son manejadas *in situ*, y 12 especies son cultivadas. Aspectos tales como la calidad y disponibilidad de los productos útiles de las cactáceas columnares, su importancia en la subsistencia humana, así como la viabilidad con la que pueden ser manipuladas, son todos factores que influyen sobre el tipo de manejo de estas plantas. Con base en un patrón de domesticación *ex situ* e *in situ* actuando simultáneamente, observado en *Stenocereus stellatus*, se propone la hipótesis de que tal patrón podría presentarse también en especies de cactáceas columnares de crecimiento relativamente rápido y con propagación vegetativa. Se discute también un patrón hipotético de domesticación *in situ* actuando solo en especies de cactáceas columnares gigantes. Estudios de biología comparativa de poblaciones silvestres y manipuladas podrían dar información sobre las tendencias y magnitud de los cambios bajo domesticación, y así conducir a un mejor entendimiento de la naturaleza y antigüedad del proceso.

Palabras clave: cactáceas columnares, domesticación, etnobotánica, Mixteca, Tehuacán

RÉSUMÉ.— Information ethnohistorique et ethnobotanique sur les espèces de cactacées columnaires utilisées et manipulées par les peuples indigènes du versant Pacifique du sud du Mexique est présentée. Cette région comprend la plus grande diversité d'espèces de cactacées columnaires du monde, avec 45 des 70 espèces mexicaines de Pachycereeae et Cereeae, dont la plupart son des espèces utiles. Bien que les cactacées columnaires ont été utilisées par les habitants de la région pendant des milliers d'années, des registres archéologiques ou historiques sur sa manipulation par des êtres humains dans le passé n'ont pas été trouvés. Dans l'actualité, désormais, même si la plupart des espèces de cactacées columnaires son exclusivement récoltées a partir de populations sauvages, certaines espèces sont en plus manipulées par les gens. En fait, les populations sauvages de 18 espèces son manipulées *in situ*, et 12 espèces sont cultivées. Des aspects tels comme la qualité et la disponibilité des produits utiles des cactacées columnaires, leur importance pour la subsistence humaine, et la viabilité avec laquelle elles peuvent être manipulées, son les facteurs qui agissent sur le genre de manipulation de ces plantes. Des modèles de façons de domestication qui pourraient avoir lieu *ex situ* ou *in situ* pour certaines espèces de cactacées columnaires son discutées. Des études de biologie comparative de populations sauvages et manipulées pourraient donner de l'information sur les tendances et la magnitude des changements sous domestication, et nous mener ainsi à une meilleure compréhension de l'antiquité de ce processus.

Mots-clés: cactacées columnaires, domestication, ethnobotanique, Mixtec, Tehuacan.

INTRODUCTION

Cacti and human cultures in the south Pacific slope of Mexico.— The south Pacific slope in south-central Mexico, including part of the states of Michoacán, México, Morelos, Guerrero, Puebla and Oaxaca (Figure 1), has been identified as the richest area in species of columnar cacti of the world, with nearly 45 of the approximately 70 species of the tribes Pachycereeae and Cereeae of Mexico occurring there (Valiente-Banuet *et al.*, 1996). Thorn-scrub and tropical deciduous forests constitute the most

common vegetation types in the area, and these are commonly dominated by columnar cacti. Archaeological studies in the Tehuacán Valley (MacNeish, 1967, 1992) and Guilá Naquitz, Oaxaca (Flannery, 1986), suggest that the region was inhabited by human beings probably from 12,000 years B. P. These studies also found in the area evidence of the earliest signs of plant domestication in the New World. At present, nearly 19 indigenous ethnic groups live there (Table 1) (see Valdés y Menéndez, 1987). This information thus reveals that the south Pacific slope includes landscapes with a high diversity and abundance of columnar cacti, as well as a considerable diversity of human cultures with a long history of experience in plant management to which columnar cacti have been important resources and cultural elements.

Since ancient times, peoples of the south Pacific slope used a broad spectrum of plant and animal resources with cacti being among the most important because of their abundance, easy accessibility and diversity, offering a great variety of resource options to the ancient gatherers. For example, in the Tehuacán Valley alone, Dávila *et al.* (1993), as well as Arias, Gama and Guzmán (1997) identified nearly 81 cactus species, all of them offering actual or potential edible products (Casas and Valiente-Banuet, 1995).



FIGURE 1.— The South Pacific slope of Mexico.

TABLE 1.— Indigenous ethnic groups from the southern Pacific slope of Central Mexico.

Ethnic group	Distribution within the region
Amuzgo	Guerrero, Oaxaca
Chatino	Oaxaca
Chinantec	Oaxaca
Chontal de Oaxaca	Oaxaca
Cuicatec	Oaxaca
Huave	Oaxaca
Ichcatec	Oaxaca
Mazahua	Michoacán, México
Mazatec	Oaxaca
Mixtec	Oaxaca, Puebla, Guerrero
Mixe	Oaxaca
Nahua	Oaxaca, Puebla, Guerrero, Michoacán, México, Morelos
Otomi	Puebla, México
Chocho-Popoloca	Puebla, Oaxaca
Purépecha	Michoacán, Guerrero
Tlapanec	Guerrero
Triqui	Oaxaca
Zapotec	Oaxaca
Zoque	Oaxaca

Smith (1967) reported remains of nine cactus species (Table 2) from archaeological excavations in the Tehuacán Valley and remains of *Opuntia* sp. from Guilá Naquitz (Smith, 1986). Among the species identified, the columnar cacti are at present important plant resources in the region. However, because archaeological remains of these cacti were not abundant in the floor of the caves studied, Smith (1967) considered that they were not significant items of the diet of ancient people. But this information contrasts with that found in human coprolites by Callen (1967) who, based on characteristics of seeds and crystals in stem tissue, distinguished the following types of cactus remains: 1) "*Opuntia* spp.", 2) "*Lemaireocereus*" (species of the columnar cacti genera *Pachycereus* and *Stenocereus* according to current nomenclature) and 3) "cactus tissue" (unidentified cacti, including possibly columnar cacti). In the earliest coprolites found, from the El Riego phase (6,500-5,000 B. C.), Callen identified the three types of cactus remains to be part of a wild food diet along with *Setaria* seeds, pochote roots (*Ceiba parvifolia* Rose), maguey leaves (*Agave* spp.) and meat. In the Coxcatlán phase (5,000-3,500 B.C.), stem tissue and fruits of "*Opuntia*" and "*Lemaireocereus*" were equally dominant material. According to Callen (1967), in the Abejas (3,500-2,300 B.C.), Ajalpan (1,500-900 B.C.), Santa María (900-200 B.C.), Palo Blanco (200 B.C.-A.D. 700) and Venta Salada (A.D. 700-1,540) phases, consumption of "*Lemaireocereus*" stem tissue, fruits and seeds could be more important than products of "*Opuntia*", and during Ajalpan and Santa María phases, "*Lemaireocereus*" could be the principal plant constituents in human coprolites.

TABLE 2.—Archaeological remains of cacti from the Tehuacán Valley (based upon MacNeish, 1967 and Smith, 1967).

Phase	Ajuereado	El Riego	Coxcatlán	Abejas	Purrón	Ajalpan	Sta. María	Palo Blanco	Venta Salada
Radiocarbon date (years B.P)	14 000-8 800	8 800-7 000	7 000-5 400	5 400-4 300	4 300-3 500	3 500-2 800	2 800-2 150	2 150-1 300	1 300-500
<i>Cephalocereus hoppenstedtii</i> ¹		X	X		X		X		
<i>Echinocactus platyacanthus</i>		X						X	
<i>Escontria chiotilla</i> ¹			X					X	
<i>Ferocactus latispinus</i>								X	X
<i>Myrtillocactus geometrizans</i> ¹			X					X	X
<i>Opuntia</i> spp.	X	X	X		X	X	X	X	X
<i>Pachycereus hollianus</i> ¹		X	X	X				X	
<i>Pachycereus weberi</i> ¹		X	X	X				X	
<i>Stenocereus stellatus</i> ¹		X	X	X				X	

¹Columnar cacti

According to Callen (1967), remains of raw stem tissue and fruits of "*Lemaireocereus*" were found in all the phases, suggesting a direct consumption of these plant products. However, in the Coxcatlán phase seeds of "*Lemaireocereus*" appear to have been eaten after having been roasted. In the Palo Blanco phase, Callen observed evidence of stems of "*Lemaireocereus*" without epidermis suggesting that they were roasted to discard the charred epidermis.

Cacti and plant domestication in the south Pacific slope.— Domestication is an evolutionary process determined by human beings (see Darwin, 1859, 1868; Schwanitz, 1966; Harlan, 1992). This process results from the continuous manipulation of morphological and physiological variation of plant and animal populations by people according to their social, economic, cultural, and technological needs. As a consequence of domestication, populations of organisms that are manipulated by people are under a continuous process of genetic divergence with respect to the original wild populations (see Hancock, 1992; Casas *et al.*, 1997a). Domestication therefore involves forms of manipulation of plant or animal populations through which people make possible the action of evolutionary forces such as artificial selection (favoring survival and reproduction of desirable phenotypes whereas undesirable phenotypes are eliminated), genetic drift (resulting from isolation of small fractions of genetic variation within manipulated populations), migration (resulting from the movement of plants and animals among localities, regions and/or continents as consequence, for instance, of human migration or commercial exchange), as well as manipulation of reproduction systems.

There is no evidence from archaeological remains that any of the cactus species were cultivated nor that their populations were manipulated in any other form within the south Pacific slope. However, ethnobotanical research in the study area by Caballero & Mapes (1985); Casas, Viveros and Caballero (1994); and Casas *et al.* (1996, 1997b) has revealed that at present there here exists a wide spectrum of forms of interactions between humans and plants, including columnar cacti, and that some of them could have derived from similar forms of plant management practiced by people in the past. Casas *et al.* (1996) group these forms of plant management into those occurring in wild plant populations *in situ* and those occurring *ex situ*. Through management *in situ*, humans may take products from nature without significant perturbations, as in some types of gathering. But also, they may alter the structure of plant populations thereby increasing the quantity of target species or particular phenotypes. These are cases of 1) "tolerance", or practices directed to maintain within man-made environments useful plants that existed before the environments were transformed by humans; 2) "enhancement", which includes the sowing of seeds or the propagation of vegetative structures of plants in the same places occupied by wild populations in order to increase numbers of useful plant populations; and 3) "protection" or conscious activities such as the elimination of competitors and predators, fertilization and/or pruning to safeguard critical wild plants (see examples of these forms of management in Casas and Caballero, 1996; Casas *et al.*, 1996, 1997a; 1997b). On the other hand, plant management *ex situ* includes interactions taking place outside natural populations, in habitats created and controlled by humans. They usually occur with domesticated plants, but it is also possible to find them occurring with wild plants. The

main forms of plant management *ex situ* are: 1) transplantation of complete individuals and 2) sowing and planting of sexual or vegetative propagules (see Casas *et al.*, 1996).

Domestication commonly occurs among plants cultivated *ex situ*, although not all cultivated plants are necessarily under domestication processes (see Harlan, 1975, 1992). However, some forms of artificial selection have been identified to occur also under *in situ* forms of plant management. Gatherers usually distinguish individual plants of some species which are different in features related to quality of food, such as flavor, size, color, presence of toxic substances, etc., and choose the best plants to use (Casas and Caballero, 1996; Casas *et al.*, 1996, 1997a, 1997b). The edible wild plant species and the preferred variants, are tolerated, enhanced and/or protected *in situ* when they are found during the clearing of forest areas, whereas those species and variants whose edible parts are not preferred by people, are eliminated. The effect of this form of artificial selection, as well as other evolutionary forces determined by human beings under forms of management *in situ*, is yet to be documented. However, in the cases of *Anoda cristata* (L.) Schl., *Crotalaria pumila* Ortega, *Leucaena esculenta* (Moc. Et Sessé ex A.DC.) Benth. and *Stenocereus stellatus* (Pfeiffer) Riccobono which have been studied in the region, Casas *et al.* (1997a) found evidence that artificial selection *in situ* has produced significantly higher frequencies of favorable phenotypes in tolerated populations when compared with wild populations. Particularly in the cases of *L. esculenta* (Casas and Caballero, 1996) and *S. stellatus*, (Casas, Valiente-Banuet and Caballero, 1998; Casas *et al.* 1998, 1999a), through multivariate statistical analyses it was found a significant morphological divergence between wild, managed *in situ* and cultivated *ex situ* populations. These analyses also revealed that such divergence is strongly determined by morphological characters used by people in folk classification of variants, in assessing quality of products, and in selecting individuals for preferential propagation, that is, those characters that are direct targets of artificial selection. This information strongly suggests that artificial selection is causing morphological (and presumably also genetic, see Casas *et al.*, 1999a, 1999b) divergence through both cultivation *ex situ* as well as management of wild populations *in situ*, and that domestication *in situ* and *ex situ* are ongoing processes in some plant species in the south Pacific slope.

Objectives.— This research aimed at examining in a historical perspective cultural aspects about use, management, traditional classification and role of columnar cacti in the economy of peoples of the region. The purpose was to document and analyze possible processes of artificial selection occurring on these plant species, how such processes might be operating, which factors are influencing this process at present, and how this could have occurred in the past.

METHODS

Ethnohistorical information.— Codices and chronicles of the Conquest and the Colonial periods for the region were reviewed to extract the historical information on use and management of columnar cacti. In some cases, attempts to identify the

species referred to in such documents were carried out based upon the descriptions and illustrations included on them.

Ethnobotanical studies.— A survey was conducted among indigenous peoples of the south Pacific slope in order to investigate patterns of management and mechanisms of artificial selection on different species of columnar cacti. Information on factors influencing the different ways of management such as forms of use, spatial and temporal availability and role in human subsistence of their useful products was emphasized. This information stressed morphological features of the different species and variants preferred for different purposes, as well as the destination of products of columnar cacti and their role in the economy of the household. Semi-structured interviews were conducted with a total of 12 Nahuatl, Mixtec and Chocho-Popoloca key native consultants in order to elicit folk classification of cacti among these indigenous ethnic groups of the Tehuacán-Cuicatlán Valley. People interviewed were from the Nahuatl villages of Coxcatlán and Rancho El Aguaje, Municipality of Coxcatlán, Puebla; the Mixtec village of Santa Catalina Chinango, Municipality of San Pedro y San Pablo Tequixtepec, Oaxaca, in La Mixteca Baja; and the Chocho-Popoloca villages of Los Reyes Metzontla and San Juan Raya, Municipality of Zapotitlán de las Salinas, Puebla.

The ethnobotanical information was complemented with data for the species studied from the Banco de Información Etnobotánica de Plantas Mexicanas (BADEPLAM) of the Botanical Garden at the Instituto de Biología, Universidad Nacional Autónoma de México and from bibliographical sources, especially from Bravo-Hollis (1978), Casas (1997) and Casas *et al.* (1997b).

RESULTS

Historic records on use and management of columnar cacti.— The “General and Natural History of the Indies” is one of the earliest written documents including information on columnar cacti. It was published by Hernández de Oviedo y Valdés, the first chronicler of the New World, in 1535. In chapter XXVI, this author wrote in old Spanish: “De los Cardones en que nasce la fructa que llaman pitahaya. No es mala fructa ni dañosa y es de buen parecer a la vista. Los cardones en que nascen estas pitahayas, es cosa fiera e de mucha salvajez la forma de ellos, los cuales son verdes e las espigas, pardas o blanquecinas, y la fructa colorada” (“About the thistle-like plants on which the fruit called pitahaya is produced. It is not a bad nor harmful fruit and it is good looking. The thistle-like plants on which the pitahayas are produced are fierce and very savage in form. The plants are green and the spines brownish or whitish and the fruit is red”). And in another chapter: “De unos cardos altos é derechos mayores que lanzas de armas (é aun como picas luengas) quadrados y espinosos, é a los cuales llaman los Chripstianos cirios por que parecen cirios o hachas de cera, excepto en las espigas. Los cardones que los Cripstianos llaman cirios en esta isla, hay los assi mismo en otras muchas y en Tierra Firme. Estos son una manera de cardos muy espinosos é salvajes que no hay en ellos parte donde se puedan tocar sin muy fieras espigas, non obstante que la Natura se las pone por orden é á trechos una de otras con mucho concierto



FIGURE 2.— *Teonochtli*, from the De la Cruz-Badiano Codex.

é compas repetidas en su composición." ("About some thistle-like plants tall and more upright than lances of the army, squared and spiny which are called "wax candles" by the Christians because they look like candles, with the exception of the spines. The spiny plants called cirios by the Christians in this island are also present in many other islands and on the continent. These are a kind of thistle-like plant very spiny and savage, which have no part that can be touched, because of the spines. However, Nature puts the spines in order and in spaces one behind the other in a very ordered and repetitive composition").

The Barberini Codex from 1552 (De la Cruz and Badiano, 1964), included a plant called "**teonochtli**" ("prickly pear of god" in Náhuatl). This plant has been identified as a species of *Stenocereus* by Bravo-Hollis (1978). Below the drawing (Figure 2), the text in Latin can be translated as: "TEETH PAIN. The ill and carious teeth have to be picked first with a tooth of a cadaver. Then, the root of a tall shrub called *teonochtli* is milled and roasted, along with deer antler and the following fine stones: *iztac quetzalitzli* and *chichiltic tapachtli*, with a small portion of flour

mixed with salt. All these things are heated. All this mixture is covered with a cloth and is applied for a brief time clenching with the teeth, especially the ill or carious ones. Finally, a mixture is made with white incense and a kind of oil called *xochiocotzol* and this is burned on live coal and its odor is collected in a piece of cotton which is applied to the mouth with a certain frequency; or, better, it is tied to the cheek".

The Florentino Codex, made in 1547 by some of the first Náhuatl writers, was translated into Spanish by Fray Bernardino de Sahagún and published in the "History of the things of the New Spain" (Sahagún, 1970, 1985). In book II of the Florentino Codex there are many references to the use and the Náhuatl classification of plants of the genus *Opuntia*. Only two drawings and texts (not translated by Sahagún) refer to columnar cacti. Neither can be identified with certainty. The first is called "*netzolli*" (Figure 3) with an inscription in Náhuatl that can be translated as: "*Netzolli*: tasty fruit, twist, many spines, it has arms, spiny plant, hurting". Based on the drawing and the reference to the character "twist" (referring to the branches) this plant is most probably *Escontria chiotilla* (F.A.C. Weber) Rose. The second is called "*teunochtli*" ("sacred prickly pear") and the inscription can be translated as: "*Teunochtli*: It has big fruits with spines, light and dark green, it is cold, it calms thirst". Based on the general appearance of the plant (Figure 3) and the character "big fruits", this could be a species of *Stenocereus*. Sahagún (1985), as well as Del Barco (1988) described how harvest of fruits of columnar cacti was crucial for subsistence of some pre-Columbian and post-conquest peoples from northern Mexico with a nomadic or semi-nomadic life, who migrated from zone to zone following the seasonal abundance of cactus fruits.

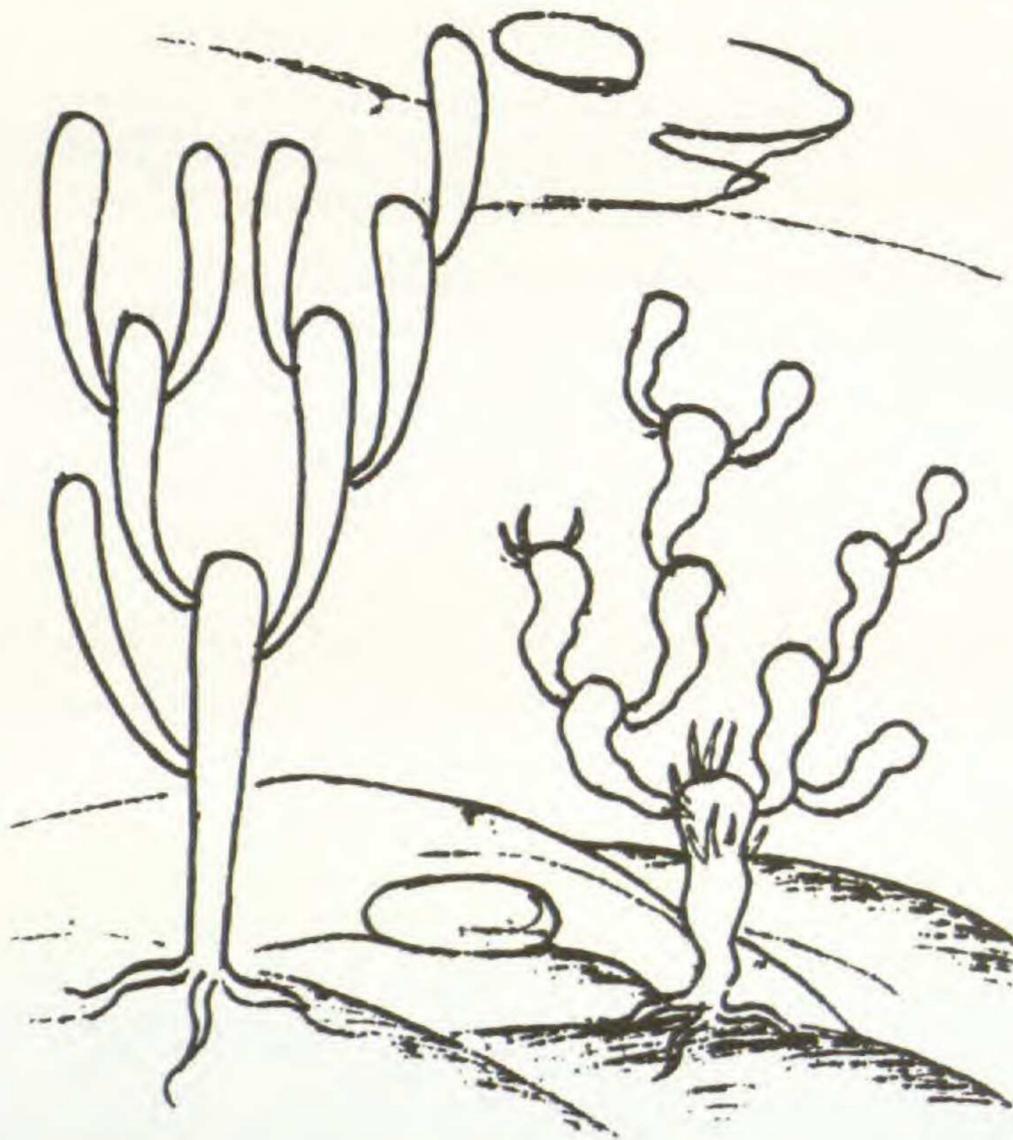


FIGURE 3.— *Netzolli* and *Teunochtli*, from the Florentino Codex

Francisco Hernández (1959), the official physician of the Spanish King Felipe II, described several species of *Opuntia*, *Ferocactus*, *Mammillaria*, *Hylocereus*, as well as *Myrtillocactus geometrizans* (C. Martius) Console and a possible *Stenocereus* species called also "*teonochtli*".

In the "Geographic Relations of the XVI Century" there are several references on the presence, use and management of *Opuntia* as well as toponymic names referring to this genus. However, the only reference to columnar cacti within the area of the south Pacific slope is found in the "Relation of Acatlán", a village near Tehuacán. This Relation, written by Juan de Vera in 1581 (Acuña, 1985), refers to the "*teonochtli*", which is found in chapter 22 in which the wild trees are described: "Hay otro árbol silvestre llamado *teonochtli*, que son unos cardones grandes, que lleva una fruta llamada pitahayas, muy gustosa y agradable, su madera arde como tea, y se sirven della para alumbrarse." ("There is another wild tree called *teonochtli*, which is a big spiny plant with a fruit called pitahayas, very tasty and nice; its wood burns like a candle, and people use it for lighting"). This plant could be *Polaskia chichipe* (Rol.-Goss.) Backeberg, the only local columnar cactus species used at present as a candle.

Ethnobotanical information.— In the study area, nearly 40 species of Pachycereeae can be found (Bravo-Hollis, 1978; Dávila *et al.*, 1993; Valiente-Banuet *et al.* 1996) (Table 3). All of these species produce edible fruits that may be collected and consumed by people. Nearly half of these species are giant columnar cacti, 10-15 m tall, characterized by a slow vegetative growth, flowering for the first time several decades after seed germination and, according to local people, for these reasons they have not been cultivated (species with habit "G" in Table 3). However, 20 species are of smaller height (2 to 8 m), relatively fast vegetative growth (the first flowering occurring 6 to 10 years after seed germination or 2 to 4 years after vegetative propagation), with most of these having clonal propagation and, according to local people, for these reasons they have been viable for cultivation (species with habit "S" in Table 3). Among these species, an exceptional morphological variation, apparently associated with human management, can be observed in fruits of *Stenocereus stellatus*, *S. pruinosus*, *S. griseus*, *S. fricci*, *S. queretaroensis*, *S. treleasei*, *Escontria chiotilla*, *Pachycereus hollianus*, *P. marginatus* and *Myrtillocactus geometrizans*.

Uses.— Food. Columnar cacti are used mainly for their fruits, which may be consumed as both fresh and dried "pasados" fruits, used for preparing jams (use "1" in Table 3). Although fruits of all species are sometimes consumed by people, it is possible to distinguish: 1) those species producing juicy sweet fruits, which are considered in this study to be "good quality fruits" which are preferred for harvesting; 2) those species considered as "regular quality fruits", which are only occasionally gathered. These include species whose fruits are difficult to obtain due to scarcity of individual plants or populations, or because branches are too tall. Also included are those species whose fruits are difficult to consume because of long or abundant spines and persistent areoles, or with not very good flavor; and 3) those species whose fruits lack juicy pulp and are rarely consumed.

Seeds of the columnar cactus species indicated in Table 3 (use "2") are con-

TABLE 3.—Species of Pachycereae from the southern Pacific slope of Central Mexico. Uses: 1 = edible fruits (*regular quality, **good quality); 2 = edible seeds; 3 = edible stems and flowers; 4 = fodder; 5 = alcoholic beverages; 6 = house construction; 7 = living fences. Habits: G = giant columnar cacti; S = small columnar cacti. Cultural status: W = wild; M = managed *in situ*; C = cultivated. Destination of products: H = consumption by household; C = commercialization.

Genus	Species	Common Spanish name	Uses	Habit	Cultural status	Destination of products	Distribution within the area
<i>Backebergia</i>	<i>B. militaris</i> (Audot) Bravo ex Sánchez-Mejorada		1, 4	G	W	H	Gro, Mich
<i>Cephalocereus</i>	<i>C. apicicephalum</i> Dawson		1, 4	G	W	H	Oax
	<i>C. chrysacanthus</i> (Weber) Britton & Rose		1*, 4	G	W	H	Pue, Oax
	<i>C. collinsii</i> (Britton & Rose) Knuth		1*, 4	S	W	H	Oax
	<i>C. guerreronis</i> (Backeberg) Buxbaum		1, 4	S	W	H	Gro
	<i>C. hoppendstedtii</i> (Weber) Schumann	cardón viejo	1*, 4, 6	G	W	H	Pue
	<i>C. nizandensis</i> (Bravo et MacDougall) Buxbaum		1, 4	G	W	H	Oax
<i>C. palmeri</i> Rose var. <i>Sartorianus</i> (Rose) Krainz		1*, 4	G	W	H	Oax	
<i>C. purpusii</i> Britton & Rose	viejo	1, 4	S	W	H	Mich	
<i>C. quadricentralis</i> Dawson		1, 4	S	W	H	Oax	
<i>C. totolapensis</i> (Bravo et MacDougall) Buxbaum		1, 4	G	W	H	Oax	
<i>Escontria</i>	<i>E. chiotilla</i> (Weber) Rose	chiotillo	1**, 2, 3, 4, 5, 7	S	W-M	H-C	Pue, Oax, Gro, Mich
<i>Mitrocereus</i>	<i>M. fulviceps</i> (Weber) Backeberg ex Bravo	cardón	1*, 4, 6	G	W	H	Pue, Oax
<i>Myrtillocactus</i>	<i>M. geometrizans</i> (Martius) Console	garambullo	1**, 4, 5, 7	S	W-M	H-C	Gro Oax, Mich
	<i>M. schenkii</i> (Purpus) Britton & Rose	vichishovo	1**, 4, 5, 7	S	W-M	H-C	Pue, Oax
<i>Neobuxbaumia</i>	<i>N. macrocephala</i> (Weber) Dawson	cardón	1, 4, 6	G	W	H	Pue
	<i>N. mezcalaensis</i> (Bravo) Backeberg	cardón	1**, 2, 3, 4, 6	G	W	H	Pue, Oax, Mor Mich, Gro
	<i>N. multiareolata</i> (Dawson) Bravo		1, 4	G	W	H	Gro

<i>Pachycereus</i>	<i>N. scoparia</i> (Poselger) Backeberg	1, 4	G	W	H	Oax
	<i>N. tetetzo</i> (Coulter) Backeberg	1**, 2, 3, 4, 6	G	W	H-C	Pue, Oax
	<i>P. grandis</i> Rose	1**, 2, 4	G	W	H	Mor, Mex, Pue
	<i>P. hollianus</i> (Weber) Buxbaum	1**, 2, 4, 5, 7	S	W-M-C	H	Pue
	<i>P. marginatus</i> (DeCandolle) Berger et Buxbaum	1**, 4, 7	S	W-M-C	H	Pue, Oax, Mex
<i>Polaskia</i>	<i>P. pecten-aboriginum</i> (Engelmann) Britton & Rose	1**, 2, 4, 6	G	W-M	H	Mich, Gro, Oax
	<i>P. weberi</i> (Coulter) Buxbaum	1**, 2, 4, 5, 6	G	W-M	H-C	Pue, Oax, Gro, Mich
	<i>P. chende</i> (Gosselin) Gibson & Horak	1**, 2, 4, 7	S	W-M-C	H-C	Pue, Oax
	<i>P. chichipe</i> Backeberg	1**, 2, 4, 7	S	W-M-C	H-C	Pue, Oax
	<i>S. dumortieri</i> (Scheidweiler) Buxbaum	1**, 2, 4, 5, 6	G	W-M	H-C	Oax, Mor, Gro, Mich
<i>Stenocereus</i>	<i>S. griseus</i> (Haworth) Buxbaum	1**, 2, 3, 4, 5, 7	S	C	H-C	Pue, Oax, Gro
	<i>S. pruinosus</i> (Otto) Buxbaum	1**, 2, 4, 5, 6	S	W-M-C	H-C	Pue, Gro Oax
	<i>S. stellatus</i> (Pfeiffer) Riccobono	1**, 2, 3, 4, 5, 7	S	W-M-C	H-C	Mor, Pue, Oax, Gro
	<i>S. treleasei</i> (Vaupel) Backeberg	1**, 2, 4, 7	S	W-M-C	H-C	Oax
	<i>S. fricii</i> Sánchez-Mejorada	1**, 2, 4, 7	S	W-M-C	H-C	Mich
	<i>S. queretaroensis</i> (Weber) Buxbaum	1**, 4, 7	S	W-M-C	H-C	Mich
	<i>S. quevedonis</i> (González Ortega) Bravo	1**, 2, 4, 7	S	W-M-C	H-C	Mich, Gro
	<i>S. chacalapensis</i> (Bravo et Mac Dougall) Buxbaum	1**, 4	G	W	H	Oax
	<i>S. chrysocarpus</i> Sánchez-Mejorada	1**, 4	G	W-M	H	Mich
	<i>S. beneckeii</i> (Enrenberg) Buxbaum	1*, 4, 7	S	W	H	Gro, Mor, Méx,
<i>S. standleyi</i> (González Ortega) Buxbaum	1**, 2, 4, 7	S	W-M-C	H	Mich, Gro	
	marismoño					

sumed by people. In general, seeds obtained from fresh or dried fruits are washed, dried and roasted. The roasted seeds are ground with chiles, onion and tomatillo or "husk tomato" (*Physalis philadelphica* Lam.) or red tomato for preparing traditional sauces which are among the main components in the daily diet of indigenous peoples of the area. The roasted cactus seeds may also be ground into an edible paste.

Stems and flowers of the species indicated in Table 3 under use "3" are occasionally eaten. Stems of columnar cacti seem to have been a common food in the past (Callen, 1967) but at present these parts are usually eaten during seasons of food scarcity. Young stems are prepared by removing the spines, cutting them in longitudinal pieces and removing the medullar portion, then roasting them in order to remove the cuticle. The flower buds are more commonly consumed during the flowering seasons. These buds are eaten boiled and then fried with eggs, but the boiled flower buds may also be prepared with onion and vinegar. This is particularly common with *Neobuxbaumia tetetzo* but occurs also with flower buds of other columnar cacti (Table 3).

In the Tehuacán Valley, economic value of edible parts is as follows, 3-5 fresh fruits or 6-10 dried fruits of *Stenocereus stellatus* (see also Casas et al., 1997b), *S. pruinosus* or *Escontria chiotilla*; 8-10 fresh fruits or 10-15 dried fruits of *Polaskia chichipe*, *P. chende* or *N. tetetzo* and 1 liter of both fresh or dried fruits of *Myrtillocactus geometrizans* are exchanged for one liter of maize; one liter of flower buds for three liters of maize; and one liter of seeds for fifteen liters of maize. These columnar cacti seem to be at present the most economically important ones in the region.

Fodder. In general, branches of columnar cacti are cut and fed to domestic donkeys, cows and goats, after removal of the spines (use "4" in Table 3). Complete fruits or their peel are also used as fodder for pigs. Pulp, seeds and chipped peels without spines are used for feeding chickens and turkeys.

Alcoholic beverages. An alcoholic drink called "*colonche*" or "*nochoctli*" ("prickly pear pulque" in Náhuatl) may be prepared from fruits of *Opuntia* spp., as well as from the species of columnar cacti indicated in Table 3 (use "5"). For preparation of "*nochoctli*", fruit juice is separated from seeds and then left for fermentation. Flavored spirits are also prepared by mixing fruits of *Myrtillocactus geometrizans*, *M. schenki*, *Stenocereus pruinosus*, and *S. stellatus* with the sugarcane alcohol "*aguardiente*".

Material for construction. Wood of giant columnar cacti is commonly used in construction of house roofs and fences (use "6" in Table 3). People generally collect the hard vascular tissue from decayed stems and branches of old giant columnar cacti that naturally fell down in the forest.

Living fences. Individuals of 11 species (use "7" in Table 3), are commonly grown as living fences in home gardens and as barriers for soil protection in terraces of cultivated slopes.

Fuel. Dry branches of all species of columnar cacti are collected to use as fuel for cooking. However, branches of *Polaskia chichipe* and *Stenocereus stellatus*, along with wood of other plant species, mainly *Ipomoea arborescens* G. Don, are especially used

for firing pottery, because the specific heat and low amount of smoke produced when burning branches of these species are considered by people to be particularly efficient for this activity.

Traditional management.— Gathering. Peoples of the area commonly gather fruits and other useful products of columnar cacti from wild populations (cultural status "W" in Table 3). In general, people said that they gather fruits selectively, preferring larger fruits of species or variants with juicy pulp, sweeter flavor, thinner pericarp, shorter and fewer spines and deciduous areoles.

Forms of management *in situ*. Additional forms of interaction can also be observed with some of the columnar cactus species. For instance, people frequently tolerate or let stand individuals of up to 18 species of columnar cacti when they clear the vegetation for cultivating maize (cultural status "M" in Table 3). This form of management is part of a general form of management *in situ* of useful perennial plants. It is also a common practice that people sow in these areas seeds of species of legume trees and plant vegetative propagules of the columnar cacti tolerated, in order to enhance their abundance in populations. Because the individuals of these tolerated species compete with the cultivated plants, people carefully select which species are the best for sparing. Their decision takes into account the usefulness of the species to spare. In the Tehuacán Valley, for instance, according to directed interviews, people manifested their preference to tolerate different species in the following order, according to their utility: *Leucaena esculenta*, *Prosopis laevigata* (Humb. and Bonp. Ex Willd.) M.C. Johnston, *Stenocereus stellatus*, *S. pruinosus*, *Pachycereus hollianus*, *P. marginatus*, *Myrtillocactus geometrizans*, *Pithecellobium dulce*, *Escontria chiotilla*, *Polaskia* spp., *Pachycereus weberi*, *Beaucarnea gracilis* Lem. and *Mitrocereus fulviceps* (Weber) Backeberg ex Bravo. They also take into account the characteristics of the useful products of the individuals within each species. In the case of columnar cacti, people prefer to spare mainly individuals with big fruits, sweet flavor, thin pericarp and few spines. However, the tolerance of other phenotypes is also common, especially when there are no other useful species or phenotypes competing. Sometimes, people prune the tolerated plants in order to improve conditions for growing maize.

Cultivation. A total of 12 species are cultivated (cultural status "C" in Table 3), mainly by planting vegetative parts in home gardens or in agricultural fields where they serve as living fences or as barriers to prevent soil erosion. In general, people cut vigorous branches from mature wild or cultivated individuals. Pieces of branches used for this purpose may be 20 to 150 cm long. They are left exposed to the sun for ten or fifteen days in order that the cut surface may dry, thus reducing fungal and bacterial infections. Then, the branches are planted in holes 10 to 40 cm deep with cattle or goat dung added as fertilizer before planting. They are usually planted just before the rainy season. They are eventually irrigated and ash is commonly deposited, as fertilizer, on the soil covering the main stems.

Individuals of columnar cacti cultivated in home gardens may also be derived from seedlings which grew from seeds dispersed via bird, bat or human feces. Because people generally do not recognize variants of columnar cactus species based on vegetative characteristics, decisions on eliminating or sparing individu-

als are taken after four to ten years, depending of the species managed, when the individuals first produce fruits.

Indigenous nomenclature and classification of columnar cacti.— Nahua classification. The Nahua people from the Municipality of Coxcatlán classify the cacti in six great categories (Figure 4). The first is “*nopalli*” which includes all the plants of the genus *Opuntia*; the second is “*nopal-xochitl*” (“nopal with flowers”) and includes species of epiphytes with flat stems and beautiful flowers, such as species of the genus *Nopalxochia*; the third is “*huitznahuac*” (“surrounded of spines”) or “*comitl*”

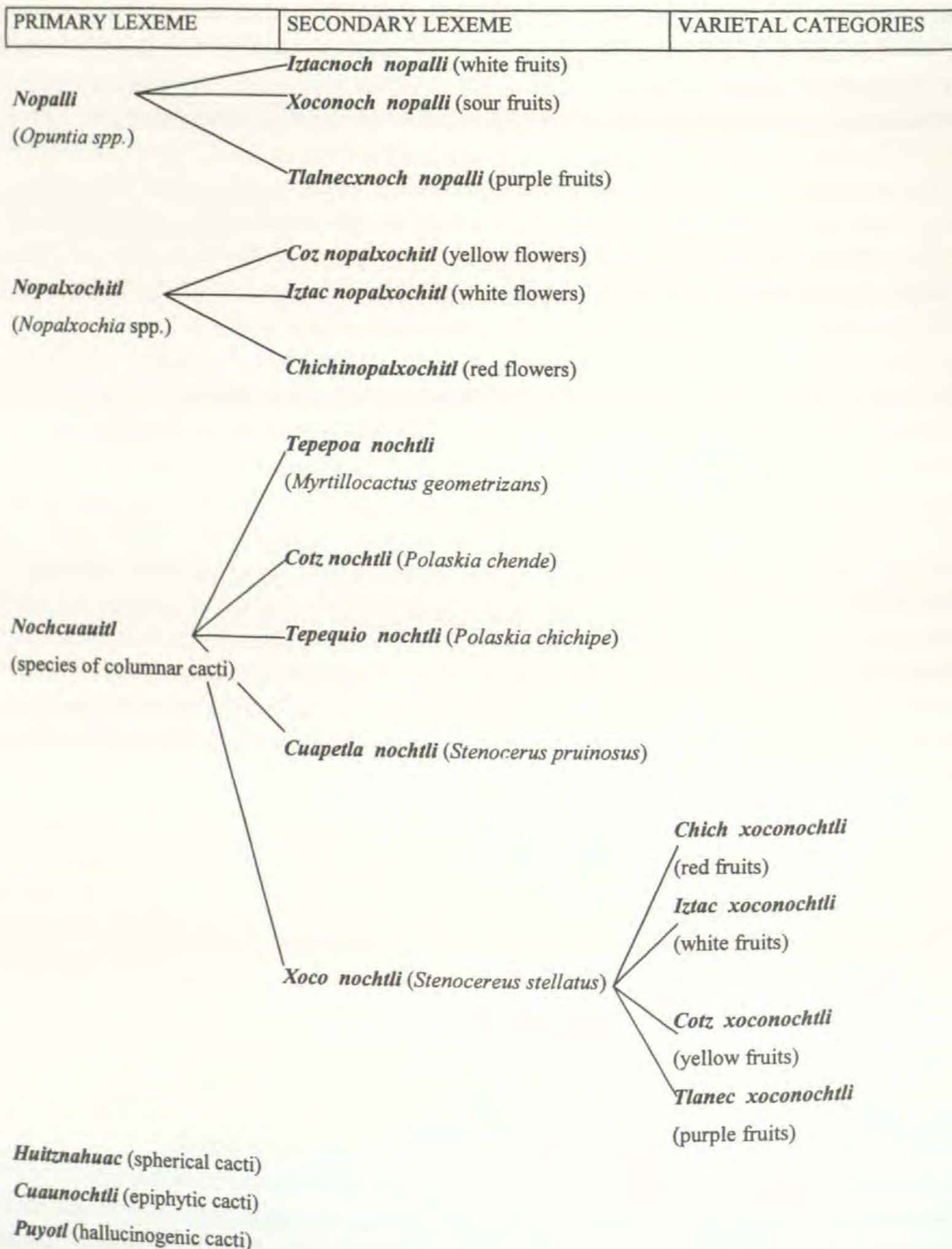


FIGURE 4.— Náhuatl system of classification of cacti.

(which refers to the form of traditional Indian pottery) which includes spherical cacti such as *Mammillaria*, *Ferocactus*, *Echinocactus*, and others; the fourth is "*cuau-nochtli*" ("prickly pear on tree") which includes several species of epiphytic cacti such as *Hylocereus*; the fifth includes species of *Lophophora* which are called "*puyotl*" (the root of the transformed word "peyote") because of their hallucinogenic properties; the sixth includes the columnar cacti and is designated by the word "*noch-cuauitl*" which means "tree producing prickly pears". It is composed by the term "*nochtli*", a word that designates the fruits of all the species of cacti and "*cuauitl*" which means tree.

The name of each of these six categories is used by the Nahua as a folk generic and an epithet, generally referring to some characteristic of a specific part of the plant, provides a folk specific. In the case of the category "*nopal-xochitl*", the flowers are the parts which are considered for naming the folk specifics. For example, the word "*cos-nopal-xochitl*" includes as a prefix the term *costic*, meaning yellow, signifying the kind of nopalxochitl with yellow flowers, indicating the cultural and cognitive significance of the flowers for the Nahua people in relation to these plants. In the case of the "*nopalli*" (*Opuntia*) and columnar cacti, fruits are the most important part used in classification. For example, terms "*iztac-noch-nopalli*", "*coz-noch-nopalli*", "*xoco-noch-nopalli*" and "*tlanecx-noch-nopalli*" designate nopalli with white, yellow, sour and purple prickly pears respectively.

In the case of columnar cacti, the Nahua of Coxcatlán use the name "*noch-cuauitl*" or more often only "*nochtli*" as a folk generic. This reveals the cultural importance of these fruits to the Nahua. For example, *Myrtillocactus geometrizans* is called "*tepe-poa-nochtli*", ("pitahaya from aggressive hills"); *Polaskia chende* is called "*cotzo-nochtli*" ("yellow pitahaya"); *P. chichipe* is called "*tepe-quio-nochtli*" ("pitahaya of scapes -*quiotl* is the term used for agave scapes- from the hills"); *Stenocereus pruinosus* is called "*cuapetla-nochtli*" ("pitahaya of big tree"); and *S. stellatus* is called "*xoco-nochtli*" ("sour pitahaya").

The first level of classification of columnar cacti by the Nahua is based on color of the pulp. In the case of "*xoco-nochtli*" (*S. stellatus*), for instance (see Casas *et al.*, 1997b), people name four variants: "*chichi-xoco-nochtli*" ("red and pink xoconochtli"), "*iztac-xoco-nochtli*" ("white xoconochtli"), "*coz-xoco-nochtli*" ("yellow or orange xoconochtli"), "*tlanec-xoco-nochtli*" ("purple xoconochtli"). They subsequently distinguish between sweet and sour flavors, using the words "*necuti*" and "*xocotl*" respectively, but these epithets never form part of the names of the plant. Similarly, they use "*uitztli*" and "*amo uitztl*" for spiny and non spiny fruits.

Chocho-Popoloca classification. Among the Chocho-Popoloca people of the Municipality of Zapotitlán de las Salinas, the classification of cacti follows a hierarchical pattern very similar to that of the Nahua (Figure 5). The term "*túchi*" ("prickly pear") is used as folk generics for grouping species of *Opuntia* and columnar cacti with big edible fruits. This term is distinguished from "*lúchi*" that includes spherical cacti. The secondary lexeme "*kánda*" groups species of the genus *Opuntia*, while each species of columnar cactus present in the area is designated by a particular name. For instance, *Stenocereus pruinosus* is designated by the name "*túchi-chína*", *Myrtillocactus geometrizans* by "*túchi-lásha*", *Polaskia chichipe* by "*túchi-cásha*" and *S. stellatus* "*túchi-kíshi*". In species of columnar cacti, as well as in *Opuntia* spp.,

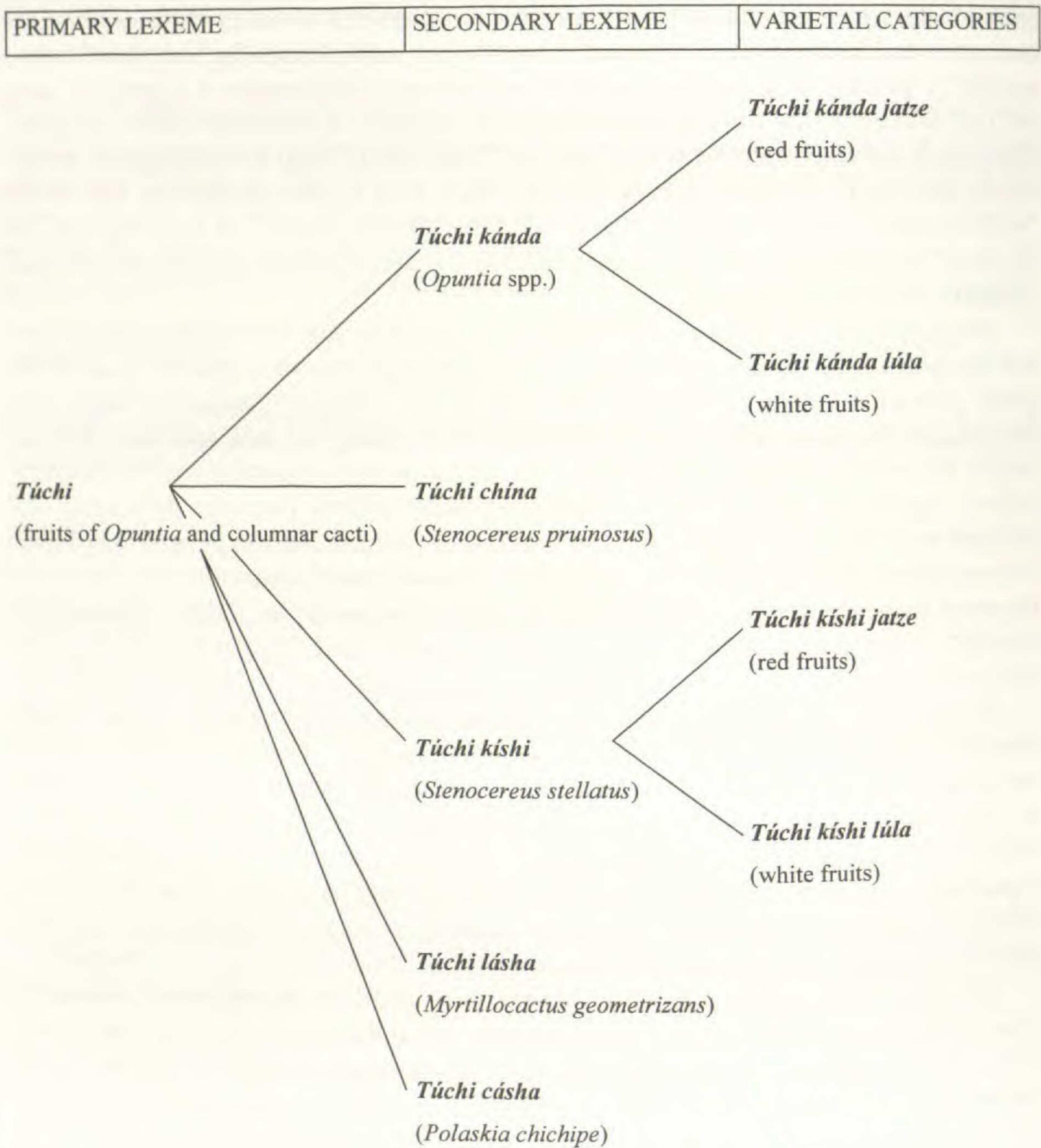


FIGURE 5.— Chocho-Popoloca system of classification of cacti.

further categories may be designated by color. In *Stenocereus stellatus*, for example "túchi-kishi-lula" and "túchi-kishi-jatze" are names used for designating variants of white and red pulp. Variants of other colors are absent in the area (Casas *et al.* 1997b). Similarly, the names "túchi-kishi-íisátu", "túchi-kishi-íshetu" and "túchi-kishi-íisan" are used to designate variants of sour, sweet and insipid flavor, respectively. Variants of spiny fruits are designated by the name "túchi-kishi-nyúñu", while the variants with few spines are designated by "túchi-kishi-canyúñu" (see also Casas *et al.*, 1997b).

Mixtec classification. The Mixtec people of the Municipality of San Pedro y San Pablo Tequixtepec classify cacti in three great groups. In one of them the term

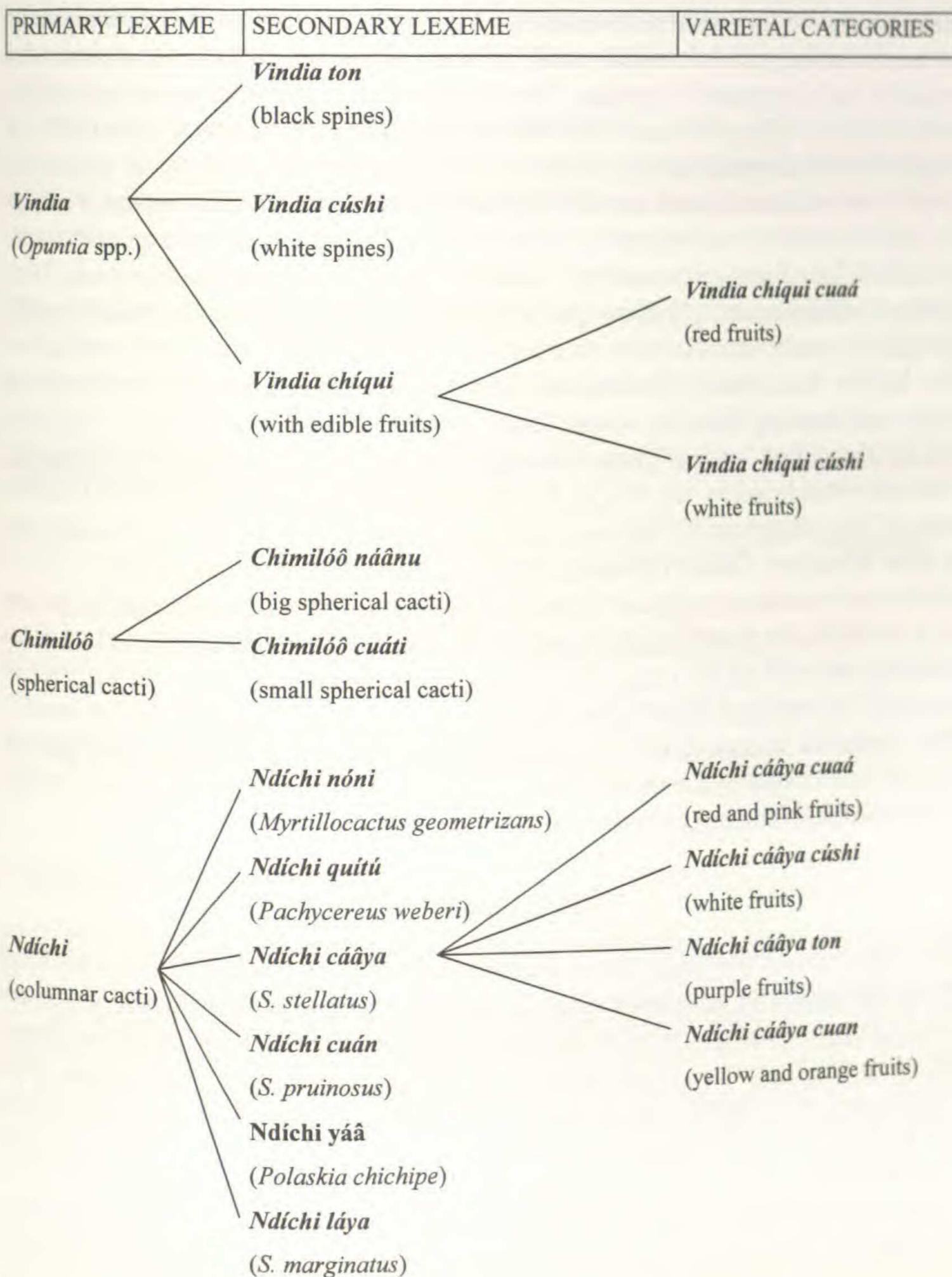


FIGURE 6.- Mixtec system of classification of cacti.

"vindia" is used as folk generics for naming *Opuntia* species (Figure 6). Specific terms may refer to characteristics of cladodes, for example "vindia-ton" ("black nopal") and "vindia-cúshi" ("white nopal") are terms referring to the presence of black and white colored spines respectively. Specific terms may also refer to characteristics of fruits which are called "chíqui". "Vindia-chíqui-cuaá" ("red prickly pear nopal"), "vindia-chíqui-cúshi" ("white prickly pear nopal") are examples of this situation. Spherical cacti are classified using the folk generics "chimilóô". People in the Mixtec region only distinguish two species of spherical cacti,

"*chimilóô-náânu*" ("big spherical cactus") in which *Ferocactus* and *Echinocactus* species are included, and "*chimilóô-cuáti*" ("small spherical cacti") which includes *Mammillaria* and *Coryphantha* species. The third main group is formed by columnar cacti classified using the term "*ndíchi*" as folk generics, which is also used for naming fruits of columnar cacti.

Species of columnar cacti are distinguished using particular terms. For example, "*ndíchi-nóni*" ("maize fruit") is used for naming *Myrtillocactus geometrizans*; "*ndíchi-quitú*" for *Pachycereus weberi*; "*ndíchi-cáâya*" ("sandy prickly pear") for *S. stellatus*; "*ndíchi-cuan*" ("yellow prickly pear") for *S. pruinosus*; "*ndíchi-yáâ*" ("white prickly pear") for *Polaskia chichipe* and "*ndíchi-laya*" for *P. marginatus*.

The Mixtec thus clearly distinguish between fruits of *Opuntia* and fruits of columnar cacti naming them as "*chíqui*" and "*ndíchi*", respectively. Fruits of spherical cacti are also called "*chíqui*", but, although they are also occasionally consumed, these are not considered by the Mixtec for the classification. Use of different names for fruits of *Opuntia* spp. and columnar cacti has also been found among the Zapotec of San Juan Mixtepec, Oaxaca (Eugene Hunn, personal communication).

Variants of columnar cacti are classified based on fruit characteristics. In the case of *S. stellatus*, for instance (see Casas *et al.*, 1997b), the first level of classification is based on color of the pulp. The Mixtec distinguish two main categories of "xoconochtli" according to their color: the red "xoconochtli" ("*ndíchi-cáâya-cuaá*") and the "colored xoconochtli" ("*ndíchi-cáâya-color*") in which they group xoconochtli with fruits of the three other colors (including white) that they recognize. They consider the red color as a wild characteristic.

DISCUSSION

Although both archaeological and historical sources indicate a continuous long history of utilization of columnar cacti by peoples of the south Pacific slope region, no evidence could be found in such sources about cultivation of these plants. In relation to the historical documents, it is difficult to accept that people who wrote them did not observe the presence of columnar cacti in the Indian home gardens as they can be seen at present. One possible explanation for this omission in the documents could be that Spaniards did not consider fruits of columnar cacti to be important resources, and for this reason they did not describe them as they did not describe many other plants. In this respect, it could be illustrative to mention that in the case of *Opuntia*, there are several references on cultivation of those species dedicated to the production of the "grana" (cochineal), a very important product for the Spaniards, but there are no references to those species dedicated to the production of prickly pear fruits. But another possible explanation for such an omission is that cultivation of columnar cacti started more recently, as suggested by Pimienta-Barrios and Nobel (1994) in the case of *Stenocereus queretaroensis*.

Additional archaeological and historical evidence is needed for answering this question, but botanical studies might also provide helpful information. These studies would allow us to examine evolutionary changes of columnar cacti under domestication by comparative analysis of morphological and genetic variation among wild and manipulated plant populations, as well as the analysis of reproductive biology and other biological aspects commonly affected by human

manipulation. This information might contribute to evaluating the extent and trends of changes under domestication and to better understanding about the antiquity of human manipulation.

The ethnobotanical information obtained indicates that at present people make decisions about how to manipulate columnar cacti species or variants according to the quality of their products, and their role in human subsistence (Figure 7). Thus, the species and variants cultivated or managed *in situ* are generally those with the most useful fruit characteristics. However, as we found in the case of *Stenocereus stellatus* (Casas *et al.*, 1997b), cultivation is particularly intensive in areas where the commercialization of fruits or their consumption by households makes necessary the production of more and or better fruits.

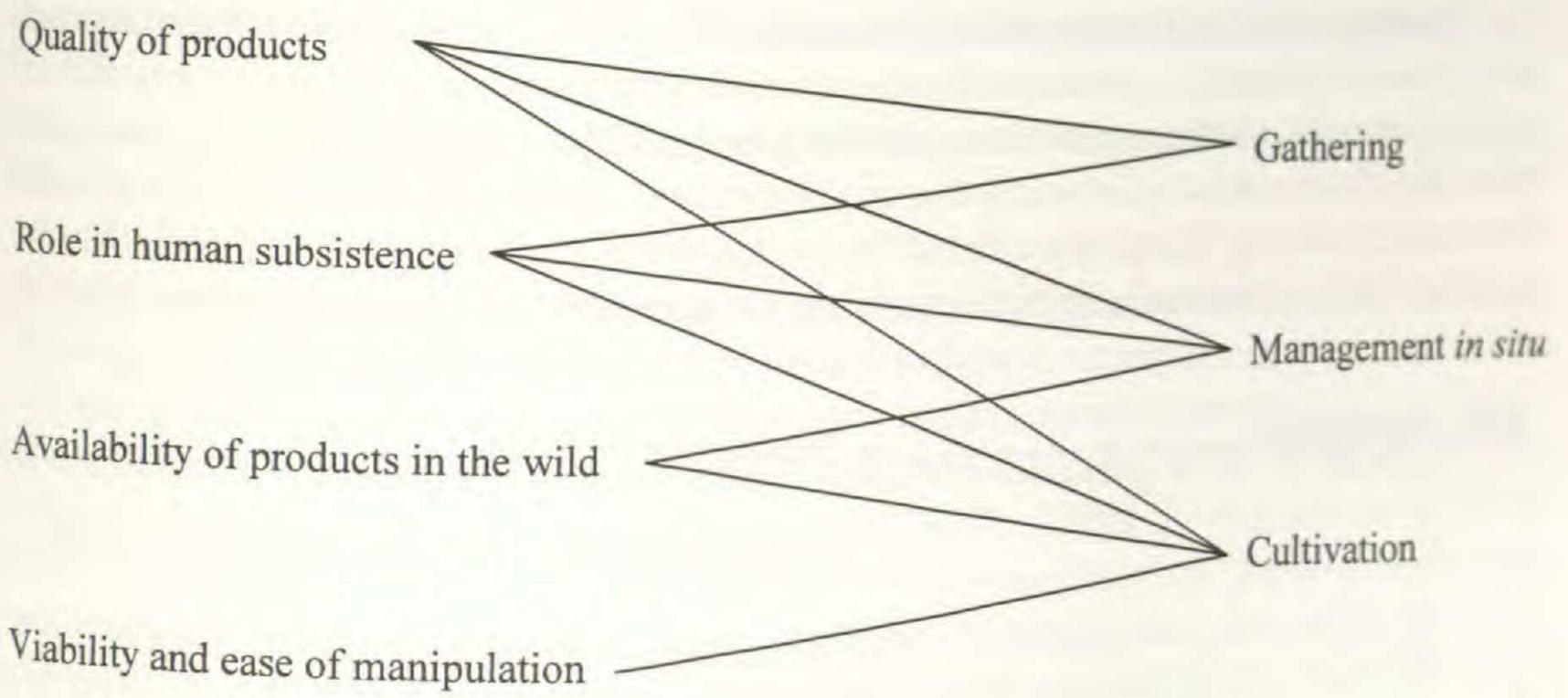


FIGURE 7.— Factors influencing types of interactions between people and columnar cacti.

Availability of plant resources is another crucial factor influencing the way they are manipulated, and this seems to be a general pattern of plant management in the area. Thus, we found that *Leucaena esculenta* and *S. stellatus* are intensively cultivated generally in places where wild populations are scarce, but not where they are abundant in the wild (Casas and Caballero, 1996; Casas *et al.*, 1997b). Also, Messer (1978) refers to a Zapotec informant who affirmed that "...we have the chipil (*Crotalaria pumila*) seeds to plant for the time when there are none in the fields so we will have greens to eat". A similar situation was observed by Casas, Viveros and Caballero (1994) among the Mixtec of Guerrero who, during the dry season, cultivate *Crotalaria pumila* and *Anoda cristata* and enhance *Amaranthus hybridus* L., in order to increase their availability.

The viability and ease of manipulation is also important. Thus, although species such as *Neobuxbaumia tetetzo*, *N. mezcalaensis*, *Mitrocereus fulviceps* and *Pachycereus weberi*, among others (Table 3), produce fruits of a very good quality, they are not cultivated *ex situ* because their slow growth makes unattractive the effort of sowing seeds and taking care of seedlings whose products most probably are not going to be seen by the sower. Slow growth may not be relevant for making decisions on managing wild populations of such species *in situ* since people simply tolerate their presence during the clearing of vegetation. However, the ef-

fect of artificial selection favoring particular phenotypes of these species *in situ* might be hardly notorious given the difficulties people have increasing numbers of desirable phenotypes by intentional direct propagation. Furthermore, when seeds of desirable phenotypes are sown, their generally outcrossing reproduction system (Casas et al., 1999b; Valiente-Banuet, *et al.* 1996, 1997a; 1997b) would make uncertain that the phenotypes selected were those expressed in the progeny sown, due to the additive genetic variance of desirable traits. On the contrary, the fixation of desirable characters in species with vegetative propagation such as *S. stellatus*, *S. pruinosus* or *S. queretaroensis* (Table 3) is relatively easy. In these species, the reproductive system is generally also outcrossing (Casas *et al.*, 1999b, Pimienta-Barrios and Nobel, 1994), but artificial selection on progeny from sexual reproduction is possible because they grow relatively fast.

Traditional classification of species and infraspecific variants of columnar cacti are generally based on characteristics of fruits, particularly size, color, and flavor of the pulp, as well as spininess and thickness of the peel. Fruits are at the same time the main useful parts and the characteristics mentioned are used by people for characterizing the quality of the fruits. Combinations of states of such characteristics may produce a broad spectrum of species and variants recognized by

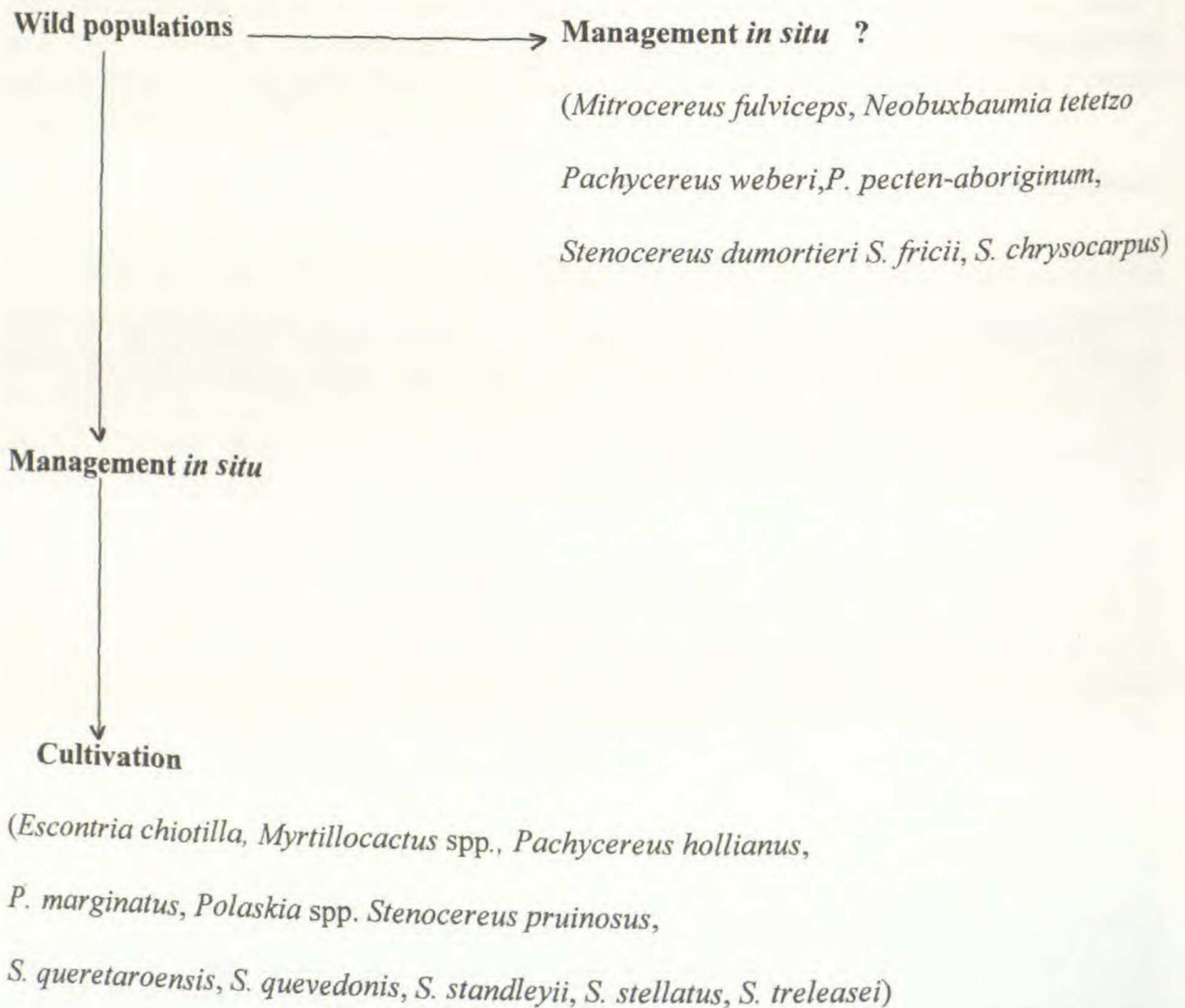


FIGURE 8.— Possible routes of domestication of columnar cacti.

people, which constitute the raw matter for artificial selection at plant community or species level. Artificial selection is apparently carried out by identifying and subsequently increasing by vegetative propagation the frequency of individuals with desirable phenotypes from wild, managed *in situ* or cultivated populations. Vegetative propagation is carried out by carrying branches of the desirable plants, wild or cultivated, to home gardens. But artificial selection apparently also occurs when plants of desired forms are preferentially spared or protected when land is cleared and non-desired plants are eliminated. A similar form of selection appears to occur when seedlings are spared by people in cultivated populations until their fruits can be evaluated, after which plants are either retained or discarded.

This information suggests that artificial selection is a potential or actual process that may act on species that are cultivated. Artificial selection has caused significant divergence between wild and manipulated populations in species such as *Stenocereus stellatus* and *S. queretaroensis* as has been documented by Casas (1997), Casas *et al.* (1999a, 1999b) and Pimienta-Barrios and Nobel (1994, 1998), and might also be significant in species such as *Myrtillocactus geometrizans*, *M. schenki*, *Escontria chiotilla*, *Pachycereus hollianus*, *P. marginatus*, *Polaskia chichi*, *P. chende*, *Stenocereus fricci*, *S. griseus* and *S. pruinosus*, among others, which are intensely cultivated and managed *in situ* and have important morphological variation in characters that are targets of selection by people. However, the demonstration and evaluation of the extent to which these species have been domesticated is yet to be done. The case study of *Stenocereus stellatus* (Casas *et al.* 1997b, 1999a, 1999b) allows us to see that domestication under management *in situ* is an ongoing process. This case suggests that both *in situ* and *ex situ* artificial selection may be acting simultaneously in some species (Figure 8). This pattern of *in situ* and *ex situ* domestication acting in conjunction could be similar in species of relatively fast vegetative growth and clonal propagation. But a pattern of domestication *in situ* acting alone could allow us to analyze possible processes of domestication of some species of giant columnar cacti such as *Pachycereus weberi*, *Stenocereus dumortieri*, *Neobuxbaumia tetetzo* and *N. mezcalaensis*, among others.

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LITERATURE CITED

- ACUÑA, R. (editor). 1985. Relaciones Geográficas del Siglo XVI: Tlaxcala. Tomo Segundo. Universidad Nacional Autónoma de México, México.
- ARIAS, S., S. GAMA and L.U. GUZMAN. 1997. Flora del Valle de Tehuacán-Cuicatlán. Fascículo 14. Cactaceae A. L. Juss. Instituto de Biología, Universidad Nacional Autónoma de México, México.
- BRAVO-HOLLIS, H. 1978. Las Cactáceas de México. Volume I. Universidad Nacional Autónoma de México, México.
- CABALLERO, J. and C. MAPES. 1985. Gathering and subsistence patterns among the Purhepecha Indians of Mexico. *Journal of Ethnobiology* 5:31-47.
- CALLEN, E.O. 1967. Analysis of the Tehuacán coprolites. Pp. 261-289 in *The Prehistory of the Tehuacan Valley. Volume one. Environment and subsistence*, D.S. Byers (editor). University of Texas Press, Austin.
- CASAS, A. 1997. Evolutionary Trends in *Stenocereus stellatus* (Pfeiffer) Riccobono (Cactaceae) Under Domestication Processes. Ph.D. Dissertation. The University of Reading, U. K.
- , J. L. VIVEROS and J. CABALLERO. 1994. Etnobotánica Mixteca: Sociedad, Cultura y Recursos Naturales en la Montaña de Guerrero. Instituto Nacional Indigenista- Consejo Nacional para la Cultura y las Artes, Mexico.
- , and A. VALIENTE-BANUET. 1995. Etnias, recursos genéticos y desarrollo sustentable en zonas áridas y semiáridas de México. Pp. 37-66 in *IV Curso Sobre Desertificación y Desarrollo Sustentable en América Latina y el Caribe*, G.M. Anaya and C.S.F. Díaz (editors) UNEP-FAO-Colegio de Postgraduados en Ciencias Agrícolas, México.
- , and J. CABALLERO. 1996. Traditional management and morphological variation in *Leucaena esculenta* (Moc. et Sessé ex A.DC.) Benth. (Leguminosae: Mimosoideae) in the Mixtec region of Guerrero, Mexico. *Economic Botany* 50:167-181.
- , M.C. VÁZQUEZ, J.L. VIVEROS and J. CABALLERO. 1996. Plant management among the Nahuatl and the Mixtec from the Balsas River Basin: and ethnobotanical approach to the study of plant domestication. *Human Ecology* 24:455-478.
- , J. CABALLERO, C. MAPES and S. ZÁRATE. 1997a. Manejo de la vegetación, domesticación de plantas y origen de la agricultura en Mesoamérica. *Boletín de la Sociedad Botánica de México* 61:30-47.
- , B. PICKERSGILL, J. CABALLERO and A. VALIENTE-BANUET. 1997b. Ethnobotany and domestication process in the xoconochtli *Stenocereus stellatus* (Cactaceae) in the Tehuacán Valley and La Mixteca Baja, Mexico. *Economic Botany* 51: 279-292.
- , A. VALIENTE-BANUET and J. CABALLERO. 1998. La domesticación de *Stenocereus stellatus* (Pfeiffer) Riccobono (Cactaceae). *Boletín de la Sociedad Botánica de México* 62: 129-140
- , J. CABALLERO, A. VALIENTE-BANUET, J.A. SORIANO and P. DÁVILA. 1999a. Morphological variation and the process of domestication of *Stenocereus stellatus* (Cactaceae) in Central Mexico. *American Journal of Botany* 86 (4).
- , A. VALIENTE-BANUET, A. ROJAS-MARTÍNEZ and P. DÁVILA. 1999b. Reproductive biology and the process of domestication of *Stenocereus stellatus* (Cactaceae) in central Mexico. *American Journal of Botany* 86 (4).
- DARWIN, C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- . 1868. *The Variation of Plants and Animals under Domestication*. John Murray, London.
- DÁVILA, P., J.L. VILLASEÑOR, R.L. MEDINA, A. RAMÍREZ, A. SALINAS, J. SÁNCHEZ KEN and P. TENORIO. 1993. Listados Florísticos de México. X. Flora del Valle de Tehuacán Cuicatlán. Instituto de Biología, Universidad Nacional Autónoma de México. México.

- DE LA CRUZ, M. and J. BADIANO. 1964. *Libellus de Medicinalibus Indorum Herbis. Codex Barberini. Instituto Mexicano del Seguro Social, México.*
- DEL BARCO, M. 1988. *Historia Natural y Crónica de la Antigua California. Universidad Nacional Autónoma de México, México.*
- FLANNERY, K.V. (editor). 1986. *Guilá Naquitz. Academic Press, New York.*
- HANCOCK, J. F. 1992. *Plant Evolution and the Origin of Crop Species. Prentice Hall, New Jersey.*
- HARLAN, J. R. 1975. *Crops and Man. American Society of Agronomists and Crop Science Society of America, Madison, Wisconsin.*
- _____. 1992. Origins and processes of domestication. Pp. 159-175 in *Grass Evolution and Domestication*, G.P. Chapman (editor). Cambridge University Press, Cambridge.
- HERNÁNDEZ DE OVIEDO Y G. VALDÉS. 1535. *Historia General y Natural de las Indias. Madrid.*
- HERNÁNDEZ, F. 1959. *Historia Natural de Nueva España. Universidad Nacional Autónoma de México, México.*
- MACNEISH, R.S. 1967. A summary of the subsistence. Pp. 290-231 in *The prehistory of the Tehuacan Valley. Volume one: Environment and subsistence*, D. S. Byers (editor). University of Texas Press, Austin.
- _____. 1992. *The Origins of Agriculture and Settled Life. University of Oklahoma Press, Norman and London.*
- MESSER, E. 1978. Zapotec plant knowledge: classification, uses, and communication about plants in Mitla, Oaxaca, Mexico. Pp. 121-146 in *Memoirs of the University of Michigan Museum of Anthropology 10*, K.V. Flannery and R.E. Blanton (editors). Ann Arbor, Michigan.
- PIMIENTA-BARRIOS, E. and P.S. NOBEL. Pitaya (*Stenocereus* spp., Cactaceae): an ancient and modern fruit crop of Mexico. *Economic Botany* 48:76-83.
- _____. and _____. 1998. Vegetative, reproductive and physiological adaptations to aridity of Pitayo (*Stenocereus queretaroensis*, Cactaceae). *Economic Botany* 52: 401-411
- SAHAGÚN, B. 1970. *El manuscrito 218-20 de la colección palatina de la Biblioteca Medica Laurenziana. Códice Florentino. Gobierno de la República Mexicana, México.*
- _____. 1985. *Historia general de las cosas de Nueva España. Porrúa. Colección "sepan cuantos" 300, México.*
- SCHWANITZ, F. 1966. *The Origin of Cultivated Plants. Harvard University Press, Cambridge.*
- SMITH, C.E. 1967. Plant remains. Pp. 220-225 in *The Prehistory of the Tehuacan Valley. Volume One: Environment and Subsistence*, D. S. Byers (editor). University of Texas Press, Austin.
- _____. 1986. Preceramic plant remains from Guilá Naquitz. Pp. 265-274 in *Guilá Naquitz*, K.V. Flannery, (editor). Academic Press, New York.
- VALDÉS, L.M. and M.T. MENÉNDEZ. 1987. *Dinámica de la Población de Habla Indígena (1900-1980). Instituto Nacional de Antropología e Historia, México.*
- VALIENTE-BANUET, _____, A., _____, M.C. ARIZMENDI, A. ROJAS-MARTÍNEZ and L. DOMÍNGUEZ-CANSECO. 1996. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. *Journal of Tropical Ecology* 12:103-119.
- _____, A. ROJAS-MARTÍNEZ, A. CASAS, M.C. ARIZMENDI and P. DÁVILA. 1997a. Pollination biology of two winter-blooming giant columnar cacti in the Tehuacán Valley, central Mexico. *Journal of Arid Environments* 37:331-341.
- _____, _____, M.C. ARIZMENDI and P. DÁVILA. 1997b. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalensis* and *Neobuxbaumia macrocephala*) in the Tehuacán Valley, central Mexico. *American Journal of Botany* 84:452-455.